0270-6474/83/0312-2652$02.00/0

The Journal of Neuroscience
Vol. 3, No. 12, pp. 2652–2659
December 1983

THE NEURAL SIGNAL FOR SKIN INDENTATION DEPTH

II. Steady Indentations[1]

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Received March 7, 1983; Accepted June 30, 1983

Abstract

The glabrous skin of the monkey's hand was stimulated with a waveform that indented the skin at a rate of 0.4 mm/sec, held the skin steadily or nearly steadily indented for 12 sec or longer, and then retracted back to the starting position. Recordings were made of activity in single afferent fibers in response to these stimuli. The average discharge frequency of 21 slowly adapting mechanoreceptors declined 38% during the first 12 sec of a steady indentation when the amplitude of the displacement was 0.65 mm and 36% when the displacement was 1.3 mm. When the plateau was not steady but the indentation depth gradually decreased by 15% during the 12-sec plateau period, the average decline was 47% for the 0.65-mm indentation and 46% for the 1.3-mm stimulus. When the indentation depth gradually increased by 15% during the 12-sec plateau, the discharge declined an average of 26% during the 0.65-mm indentation and 22% during the 1.3-mm displacement. To determine the effect of receptor adaptation on the perception of skin indentation depth, 13 human subjects had the skin of their fingertips indented 1 mm with similar trapezoidal waveform and were asked whether the indentation depth increased or decreased during the plateau portion of the stimulus. Ten of the 13 subjects thought that the indentation depth was increasing when the plateau was steady. The method of limits was then used to determine how much the stimulus had to change for the subject to feel the depth during the plateau as unchanging; i.e., a "perceptual zero." The average perceptual zero for the entire group occurred when the stimulator steadily retracted by 14% during the plateau. The subject whose indentation depth sensation adapted the most felt the plataeu to be steady when the stimulator gradually advanced by 15% during the plateau. A different group of 10 subjects traced the perceived depth of steady fingertip indentations which were 1 and 2 mm deep while the stimuli were actually in progress, and more than half traced a sensation of gradually increasing depth. The subject in this group whose depth sensation adapted the most showed a decline of 13% during a steady plateau 18 sec long, as compared with the average discharge of our sample of slowly adapting monkey mechanoreceptors, which declined 45% during a comparable stimulus. Tracings were also made by these subjects of waveforms that remained steady for 2 to 4 sec, partially retracted by 5 to 30%, and then reindented to the same depth. When the partial retractions were slow, the subjects thought the indentation depth increased with each repetition of the stimulus although the stimulator actually reindented to the same depth each time. The fact that human subjects tend to feel the depth of a steady indentation as increasing at a time when the discharge of their glabrous skin mechanoreceptor is declining could be explained if the adapting discharge were to be integrated (in the mathametical sense) by the central neural circuitry responsible for judgments of skin indentation depth. Such an integration process could also account for the increase in perceived depth during reindentation since present evidence indicates that receptor discharge declines rather than increases during repeated reindentations to the same depth.

[1] This work was supported by grants from the National Institutes of Health and National Science Foundation. We thank John Fisher, Barry Evans, Carol Reeves, and Vicki Skelton for their help.

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Over two decades ago, Renfrew and Melville (1960) clearly distinguished the sensation of skin indentation depth as a separate attribute of tactile sensibility. This is a spatial sensory experience in which the skin surface is felt to be displaced toward the deeper tissues of the body. Although Renfrew and Melville (1960) and Smaje and McLennan (1981) have measured the skin displacements required to elicit indentation depth sensations using methods convenient for clinical testing, it seems justified to subject indentation depth sensations to further study in view of the commonplace nature of these sensations and their likely importance for judging the curvature of objects pressing into the skin, whether delicate objects gently grasped are likely to slip from the fingers, etc. In this report the emphasis is on the consequences of receptor adaptation and fatigue for judgments of skin indentation depth.

Adaptation is a well known property of cutaneous mechanoreceptors, first described by Adrian and Zotterman (1926) and observed many times since. The decline in the input signal from the skin that results from adaptation would appear to be undesirable for any tactile sensation that requires constant maintenance during a steady stimulus. For example, if sensations of skin indentation depth are to provide reliable information during a steady indentation, it would seem necessary that they not change markedly. Early work (Zigler, 1932; Crook and Crook, 1935; Horch et al., 1975) has shown that tactile sensations do in fact disappear over a period of minutes, but in these studies, the stimuli were delivered to hairy skin, and the initial part of the adaptation process was not examined. It is the glabrous skin of the hand that is deformed during the most precise tactile behavior of primates, and often an object steadily indents the skin for only a few seconds during such behavior. We have therefore evaluated subjects' perception of skin indentation depth during the first 12 to 20 sec of a steady indentation applied to the fingertips. To our surprise we found that most subjects thought the indentation depth of a steady stimulus actually increased by varying amounts during this time. This apparently requires some compensation of the adapting receptor discharge by the central nervous system, such as could be achieved by integration (in the mathematical sense) of the receptor signals. An integrator mechanism of this type is suggested also by the fact that perceived indentation depth can be made to increase ("wind-up") by repeatedly indenting the skin to the same depth, since such stimuli cause mechanoreceptor fatigue.

Materials and Methods

Physiological studies

Two adult monkeys (*Macaca mulatta*) were anesthetized with an intraperitoneal injection of pentobarbital and were given additional doses via the radial vein as necessary to prevent withdrawal reflexes. The median nerve was exposed in the forearm under sterile conditions and covered with mineral oil. Small strands were dissected from the nerve and placed on a recording electrode so that the activity of single afferent fibers could be studied. Rectal temperature was held between 37 and 38° C with external heat. After the experiment was over, the skin was sutured, 300,000 units of penicillin were injected intramuscularly, and the animals recovered without incident.

Once a glabrous skin mechanoreceptor had been isolated, the receptive field focus was located with a von Frey hair, marked with washable ink, and indented with a flat plastic disc, 2 mm in diameter, attached to a moving coil stimulator. The moment of skin contact was determined by looking at the stimulator tip through a dissecting microscope as the stimulator was slowly advanced using a micromanipulator. After contact, the stimulator was lowered an additional 0.3 mm. The stimuli consisted of six different waveforms given in an irregular sequence. Each indented the skin at a rate of 0.4 mm/sec and, after a plateau phase, retracted at the same rate. Between the indentation and retraction phases, the displacement either remained constant for 20 sec (stationary plateau), slowly increased by 15% during a 12-sec plateau (plateau with inward "creep"), or slowly decreased by 15% during a 12-sec plateau (plateau with outward creep). Each of these three plateau configurations was tested at two amplitudes of initial plateau indentation, 0.65 mm and 1.3 mm, making a total of six stimuli. The interval between the end of one stimulus and the beginning of the next was 1 min.

The nerve impulses generated in response to these stimuli were digitized on line by a computer, together with a signal from the stimulator indicating indentation depth, and both were displayed as a function of time. Plots were made of instantaneous frequency (reciprocal or interspike interval) as well as of average frequency versus time. Adaptation during the 20-sec (stationary) plateaus was evaluated by comparing the average frequency during the first 2 sec of the plateau with the average during the 11th and 12th sec and the 19th and 20th sec of the plateau. Adaptation during the plateaus with creep was evaluated by comparing the average frequency during the first 2 sec of the plateau with the average frequency during the last 2 (11th and 12th) sec of the plateau.

Psychophysical studies

Reporting the direction of a gradually changing indentation. Thirteen human subjects of both sexes were used, ranging in age from 10 to 43 years. They knew nothing about the aims of the experiment and were told nothing about their performance until all tests were completed. They were seated comfortably with the fingers resting against a molded support of plasticine. All were tested on the middle and index fingers of the right hand and all were right handed. The stimuli were delivered to the palmar aspect of the terminal phalanx (fingertip) with a flat plastic disc 3.5 mm in diameter. The same stimulator was used as for the monkey mechanoreceptor studies, and the trapezoidal waveforms had indentation and retraction velocities of 0.4 mm/sec and 12-sec plateaus. All plateaus had an initial amplitude of 1 mm which was given from an initial (resting) indentation of 0.5 mm. The subjects could not see the moving portions of the stimulator or their fingertips, and operation of the devices was silent.

The subjects were read the following statement: "Your fingertip will be indented with a waveform that goes in fairly rapidly and also withdraws fairly rapidly. Between these more rapid phases there will be a plateau phase during which your skin will be held indented but this indentation will not be constant. There will be a slow, steady change in the depth of the indentation during this time. Your task is to determine whether the depth of the indentation gradually increases or gradually decreases during the plateau phase. If you don't think the indentation depth changed, you will be required to guess whether the slow change was in or out. To help you in making these judgments, we will tell you when the slow phase ends and the stimulator is starting to retract. Do you have any questions?" Each subject was given a few trials in the apparatus before actual testing began.

The first stimulus each subject received had a steady plateau. If the subjects said the indentation was increasing (the usual response), the next stimulus was one in which the stimulator gradually withdrew at a constant rate during the 12-sec plateau until, by the end, it had retracted 0.1 mm (10% of the initial value), and the subject again made a judgment. Ten percent increments were added to the rate of plateau retraction until the subject said the indentation was decreasing, after which the rate was increased by 10% until the subject again reversed his judgment. This process was continued until the subject had reversed judgment a total of seven times. The first reversal was discarded, leaving six for analysis. The percentage of change in plateau depth halfway between each reversal was considered to be the "perceptual zero." A similar "limits" method was used for the few subjects who thought the indentation was decreasing when the plateau was steady except that the 12-sec plateau was now increased by 10%. Thus there were five perceptual zero values available for each subject, as well as three where the subject reversed an in to an out judgment and three where an out judgment was reversed to an in judgment. The data were analyzed by averaging comparable values and comparing the means to zero using a two-tailed t test.

Tracing perceived skin indentation depth. Ten subjects were used, aged 27 to 41 years. They were not the same subjects used in the preceding test. They also did not know the aims of the experiment or the waveforms of the stimuli that would be used to indent the skin and were given no clues as to their performance until all of the tests were completed. The subjects were seated at a table with the fingers of the left hand resting against a plasticine support. All the stimuli were delivered to the fingertips of the middle or index fingers of the left hand, which was the nondominant hand for all of the subjects, with a flat, plastic disc 3.5 mm in diameter. The stimuli started from an initial (rest) indentation of 0.5 mm and all had a rising phase of 0.4 mm/sec. Subsequent portions of the waveforms differed in shape depending on the nature of the test.

Each waveform to be evaluated was delivered three to six times to the left hand of a particular subject, and for each stimulus presentation the subject moved a potentiometer with his right hand to track the perceived skin indentation depth. The potentiometer had a pointer which moved along a 30-mm scale numbered from 0 to 6 at 5-mm intervals. The subjects were read the following statement: "The skin of one of your fingertips will be indented in different ways. Your task is to move this pointer along the scale so that the position of the pointer matches your perception of the depth of the fingertip indentation. You are asked to follow this indentation depth with the pointer moment-by-moment from the beginning to the end of the stimulus. Call the initial indentation depth before each stimulus begins zero. Do you have any questions?" The subjects were given two to three trials in the apparatus before actual testing began. None showed any inclination to go off the top of the scale.

The output of the potentiometer and a signal indicating the depth of the indentation were fed into different channels of a strip chart recorder. The results were analyzed by comparing the actual waveforms with the subject's representations of their sensations. Differences in the subjects' responses to different stimuli or to different portions of the same stimulus were evaluated with the Wilcoxon matched pairs signed ranks test. The criterion for significance was $p = 0.05$ (two tailed).

Results

Physiological studies

Although adaptation is a well known property of cutaneous mechanoreceptors, it was thought desirable to make a quantitative study of its magnitude under conditions like those to be used in the psychophysical experiments. Twenty-one slowly adapting receptors were studied in the two experimental animals. Nineteen of the receptors were judged to be SAI and two to be SAII. The latter had less distinct receptive field foci, more stretch sensitivity, and a more regular discharge than did the former. Figure 1 illustrates the response of a typical SAI receptor to a stimulus with a steady plateau (Fig. 1*A*), a stimulus with a 15% outward creep (Fig. 1*B*), and one with a 15% inward creep (Fig. 1*C*). Each had an initial plateau amplitude of 0.65 mm. Figure 2 illustrates the response of one of the SAII receptors to these same stimuli. Both receptors adapted, even during the plateau with inward creep (see "Materials and Methods" for how adaptation was evaluated). The receptor with the least adaptation was the SAI illustrated in Figure 3. The discharge adapted during the steady plateau and during the plateau with outward creep. During the plateau with inward creep (Fig. 3*C*), the discharge first declined and then increased so that the average frequency during the first 2 sec of the plateau was about the same as during the last 2 sec of the plateau. Figure 4 illustrates the average response of the population of 21 units (computed as described in the figure legend) to indentation amplitudes of 0.65 mm and 1.3 mm. During a stationary 0.65-mm plateau, the average response declined 38% between the first 2 and the 11th and 12th sec and 45% between the first 2 and the 18th and 19th sec (Fig. 4*A*). The corresponding values for the 1.3-mm plateau were 36 and 48% (Fig. 4*B*). During an outward creep of 15% from an initial indentation of 0.65 mm, the discharge declined 47% between the first 2 and the 11th and 12th sec (Fig.

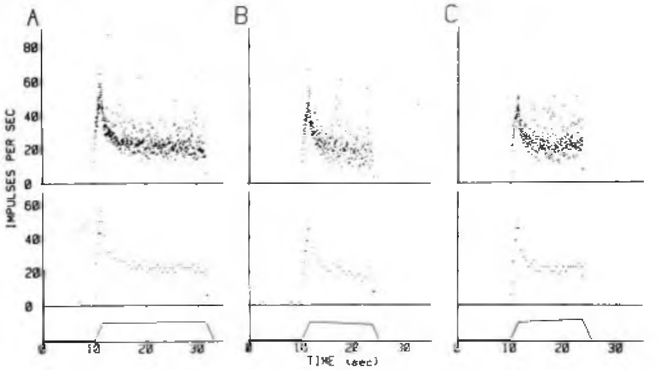

Figure 1. Responses of a typical SAI monkey mechanoreceptor are shown to a stimulus that indented the skin 0.65 mm at a rate of 0.4 mm/sec and, after a plateau phase, retracted at the same rate. In *A*, the plateau lasted 20 sec and was steady; in *B*, the plateau was 12 sec long and the indentation depth decreased by 15% during this time (outward creep); in *C*, the duration was 12 sec and the depth increased by 15% during the plateau (inward creep). The *upper records* are instantaneous frequencies (reciprocal of interspike interval). Average frequencies are shown immediately *below* the instantaneous frequency records, and the corresponding stimulus waveform is represented below the frequency traces. Average frequencies were determined by counting the number of impulses occurring in a particular time period (bin) and dividing by the bin time. The bin durations were 0.16 sec during the rising and falling phases of the stimuli and 0.5 sec on the plateaus. Unit E5-18.

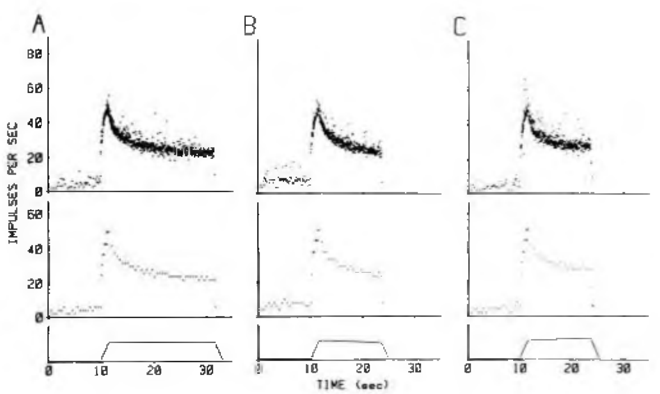

Figure 2. The responses of a SAII receptor are shown, represented as in Figure 1 and to the same stimuli. Unit E5-19.

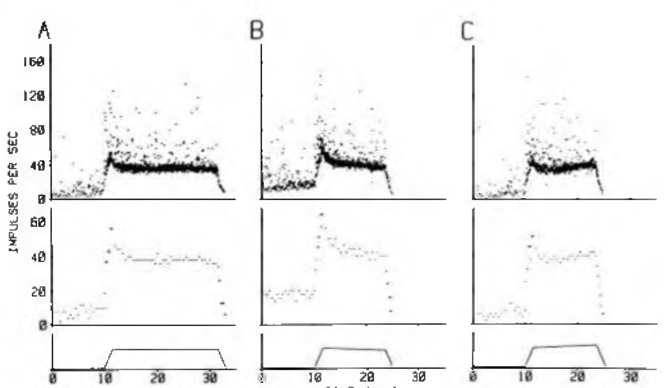

Figure 3. Responses are shown for the most tonic of the 21 slowly adapting receptors in the sample. This receptor was classified as SAI. The method of representation and the stimuli are the same as in Figure 1. Unit E5-11.

4*C*). The corresponding value for the 1.3-mm indentation was 46% (Fig. 4*D*). During an inward creep of 15% from an initial indentation of 0.65 mm, the discharge declined 26% between the first 2 and the 11th and 12th sec (Fig. 4*E*). The corresponding value for the 1.3-mm indentation was 22% (Fig. 4*F*).

Nine units in the sample were also stimulated adjacent to their receptive field foci (Fig. 5). This was accomplished by moving the stimulator 2 mm lateral to the center of the receptive field. This caused an increase in the rate of adaptation as compared with on-focus stimulation (cf. Figs. 4 and 5).

Seventy-eight slowly adapting receptors in monkey glabrous skin, whose responses to moving stimuli were described in an earlier paper (Burgess et al., 1983), were also stimulated with a 1.3-mm trapezoidal waveform that

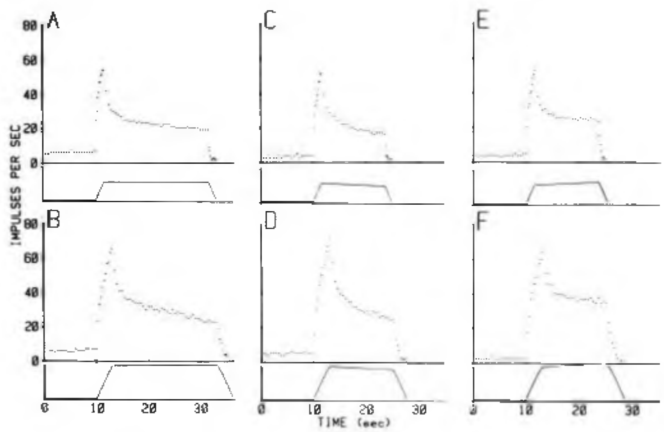

Figure 4. Average frequencies are shown for all 21 slowly adapting receptors in the population. Each waveform was delivered to each receptor once, and the numbers of impulses in comparable time bins were totaled and divided by the number of receptors contributing and the bin duration to give an average receptor response. Indentations of 0.65 mm are shown above (*A, C,* and *E*) and indentations of 1.3 mm are shown below (*B, D,* and *F*). The plateau was steady in *A* and *B*, decreased by 15% in *C* and *D*, and increased by 15% in *E* and *F*. The bin durations for averaging were 0.5 sec on all of the plateaus, 0.16 sec on the rising and falling phases in *A, C,* and *E*, and 0.32 sec on the rising and falling phases in *B, D,* and F.

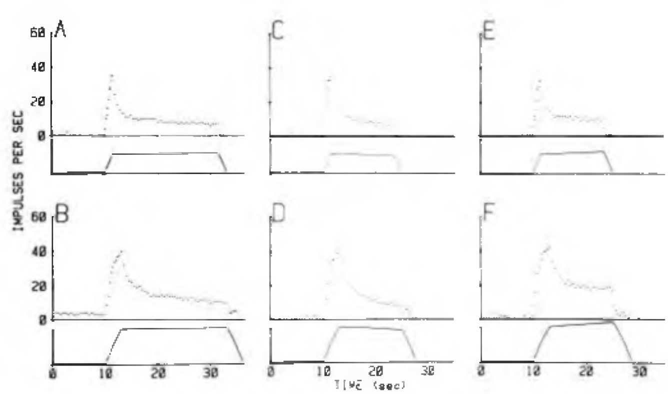

Figure 5. Average frequencies are shown for nine slowly adapting receptors that were stimulated 2 mm lateral to their receptive field centers. Stimulus waveforms and data representation are as in Figure 4.

had a 3-sec stationary plateau. Fifty-five of these receptors were classified as SAI, 20 as SAII, and 3 as intermediate, primarily on the basis of discharge periodicity. All showed adaptation during the 3-sec plateau.

Psychophysical studies

In these experiments, human subjects were tested to determine whether their perception of skin indentation depth would change during a steady indentation in a way that paralleled the declining discharge of cutaneous mechanoreceptors. In the first study, subjects verbally reported whether the stimulator was causing a gradual increase or decrease in the depth of a skin indentation, and in the second study, they traced the perceived depth of a skin indentation while the stimulus was in progress.

Reporting the direction of a gradually changing indentation. Figure 6 shows a common response; this subject (JA) felt the steady plateau as a slow indentation and did not reverse her judgment until the stimulator had been slowly withdrawn a total of 40% during the plateau (see "Materials and Methods" for a description of procedure). The stimulator retraction was then reduced in 10% increments and she reversed from an "out" to an "in" judgment when the plateau retraction had been reduced to 20%. This sequence was continued until seven reversals had occurred. With the first reversal omitted, there were three in-to-out reversals at a plateau retraction of 30%, three out-to-in reversals at a retraction of 20%, and five midpoint ("perceptual zero") values at a retraction of 25%. The subject with the most positive perceptual zero had an average out-to-in reversal during a slow increase in plateau indentation of 20% and an average in-to-out reversal at an increase of 10%, giving an average midpoint of 15%. For all of the subjects combined, the average in-to-out reversal occurred at a plateau retraction of 22%, the average out-to-in reversal occurred at a retraction of 6%, and the average midpoint was a retraction of 14%. All of these values were significantly more negative than zero ($p < 0.05$ for the out-to-in reversal and $p < 0.001$ for the others). Of the 13 subjects tested, 3 had average midpoints that were positive. For the subject with the most positive midpoint in the whole series, the average perceptual zero was a plateau increase of 15%, and for the subject with the most negative midpoint, the average perceptual zero was a retraction of 50%.

Tracing perceived skin indentation depth. Since the results of the preceding experiment were unexpected, a different group of subjects was asked to trace their perception of the depth of a skin indentation while the stimulus was in progress. This they were able to do without difficulty, and steady plateaus of varying duration were tested. Figure 7 shows records from a subject who felt a steady 2-mm indentation as gradually increasing, and the tracings in Figure 8 are from another subject who felt a steady 2-mm indentation as constant. Figure 9 shows that more than half of the subjects fell into the former category when tested with 1-mm (Fig. 9*A*) and 2-mm (Fig. 9*B*) indentations, as would have been expected from the first series of psychophysical experiments. The average perceived change for all subjects combined, from the beginning to the end of an 18-sec plateau, was an increase of 23% for a 1-mm indentation (Fig. 9*A*) and an

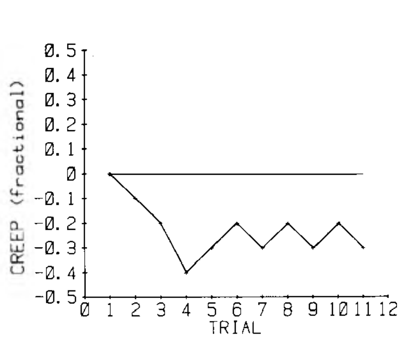

Figure 6. The response of a typical subject (JA) is shown. When the fingertip was stimulated with a 1-mm trapezoidal waveform that indented the skin at 0.4 mm/sec, held the skin steadily indented for 12 sec (plateau portion of the stimulus), and then retracted at 0.4 mm/sec, the subject felt the 12-sec steady plateau as increasing. When the outward creep on the plateau had reached 40% (*positive creep* designates indentation, *negative creep* designates retraction), the subject reversed judgments (felt the steady phase as decreasing) and thereafter felt 20% retractions as increasing and 30% retractions as decreasing in this forced choice paradigm, giving a "perceptual zero" at a retraction of 25%.

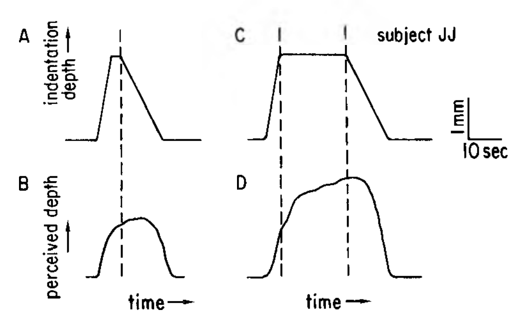

Figure 7. A and *C* show 2-mm waveforms used to indent the fingertip. *B* and *D* show the perceived changes in indentation depth produced by *A* and *C*, respectively. *B* and *D* have been shifted about 1 sec to the *left* on the time axis so that they start when the actual waveforms began. The 10-sec time calibration applies to all of the traces and the 1-mm depth calibration applies to *A* and *C*; the *ordinate* in *B* and *D* is in subjective units. The perceived depth did not start to decline until about 7 sec after the retraction in *A*, and the perceived depth increased during the steady plateau in *C*. The errors in *B* and *D* were among the largest observed.

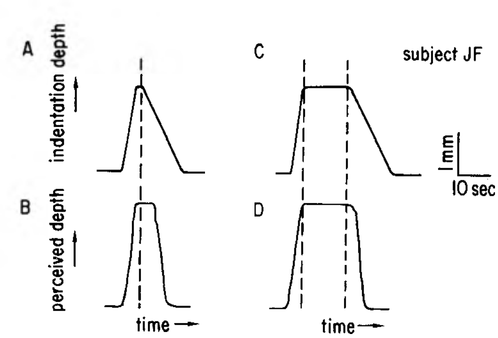

Figure 8. Stimulus waveforms and perceived indentation depth are represented as in Figure 7. For this subject, perceived indentation depth changed little during a 2-mm steady indentation.

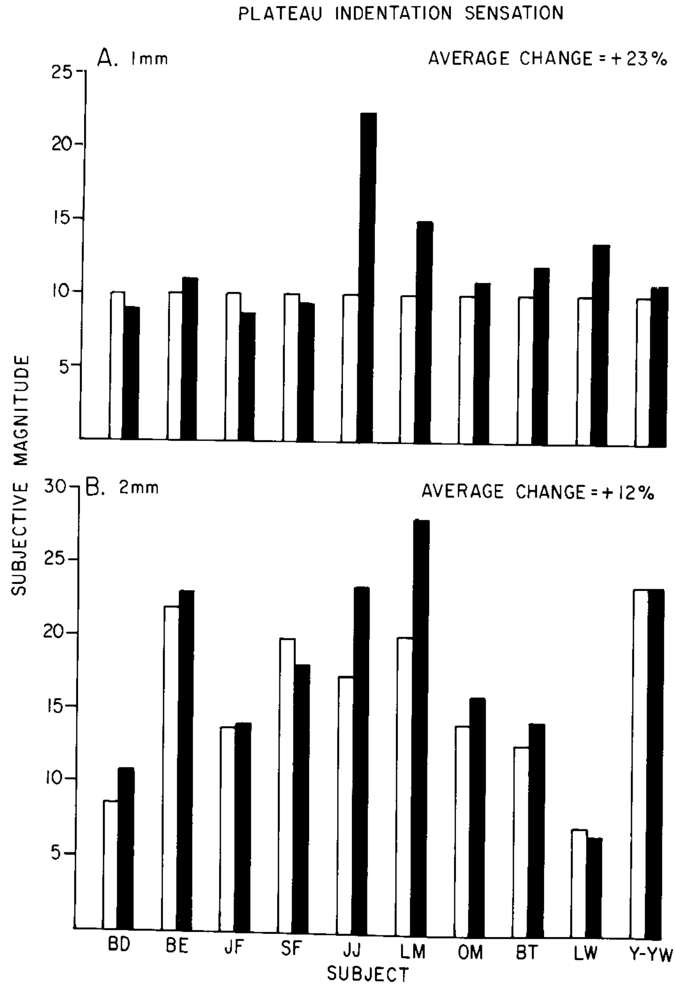

Figure 9. The *open bars* in *A* indicate the perceived indentation depth 1 sec after the skin was indented 1 mm at a rate of 0.4 mm/sec. The *solid bars* indicate the perceived depth 18 sec after the first measurement was made. The actual depth remained unchanged during this time. To facilitate comparison between subjects, each subject's initial response to the 1-mm plateau (*open bars* in *A*) was assigned a value of 10 and the responses 18 sec later (*solid bars* in *A*) were scaled relative to this value. *B* is similar to *A* except that the displacement had an amplitude of 2 mm. The responses in *B* were scaled relative to the initial response (*open bars*) for the same subject in *A*. Three to six repetitions of the stimulus were averaged to obtain each value. The average increases, 23% in *A* and 12% in *B*, were statistically significant ($p < 0.05$).

increase of 12% for a 2-mm indentation (Fig. 9*B*). Both were statistically significant ($p < 0.05$). Even the most pronounced decline in perceived depth in Figure 9 (13%, JF, 1 mm) fell well short of the 45% decline in the discharge of the average slowly adapting monkey mechanoreceptor during a similar stimulus. Not only does perceived indentation depth fail to correlate with mechanoreceptor discharge during a steady indentation, but there is also no initial overshoot in perceived depth corresponding to the overshoot in mechanoreceptor activity that occurs during the indentation phase of the stimulus (cf. Figs. 7 and 8 with Figs. 1 to 5).

In the early part of this century there were several studies on the persistence of tactile sensations after removal of the stimulus. These are referred to as primary aftersensations (Spindler, 1897; Hayes, 1912; Dimmick, 1916; Holland, 1920; Boring, 1942). Examples of indentation depth aftersensations are shown in Figures 7*B* and 8*B*. Indentation depth aftersensations were found not to occur to any extent unless the stimulator retracted sufficiently slowly that the subjects did not directly feel the retraction (note the slow retraction rates in Figs. 7 and 8); if the subjects felt the skin moving outward, the perceived depth decreased largely in time with the actual retraction.

It occurred to us that it might be possible by reindenting the skin while an aftersensation was in progress to cause perceived indentation depth to "wind-up" in the sense that a second indentation to the same depth would be felt as a deeper than the first indentation. We found that such errors were favored by a retraction rate that was as rapid as possible consistent with a good aftersensation, perhaps because a larger retraction then occurred in a given time period, allowing the immediately following indentation to be larger. On the basis of preliminary experiments, we began testing each subject with a retraction rate of 0.2 mm/sec. Trapezoids with short plateaus, like those in Figures 7*A* and 8*A*, were used to adjust the retraction rate to a suitable value for each individual subject. In some subjects the retraction rate had to be reduced below 0.2 mm/sec, sometimes to 0.05 mm/sec, to obtain a good aftersensation. In others the retraction velocity could be increased to 0.3 mm/sec with good persistence of the aftersensation. Figure 7*B* shows one of the longest aftersensations observed and Figure 8*B* shows a more typical result.

Once the appropriate retraction rate had been selected, the stimulator was allowed to retract only 5 to 30% before it was reindented to the original depth, and this was repeated several times. The tracing in Figure 10*B* is an example of the "staircase" increments usually obtained, whereas the tracing in Figure 10*D* (from another subject) shows oscillations indicating that some decrease in perceived indentation depth occurred during the retractions.

Figure 11 shows the wind-up errors for 10 subjects at plateau indentation depths of 1 mm (Fig. 11*A*) and 2 mm (Fig. 11*B*). The *open bars* in Figure 11*A* show the perceived depth of the 1-mm indentation (in normalized subjective units) just before the start of the first partial retraction. The *solid bars* show the perceived depth of

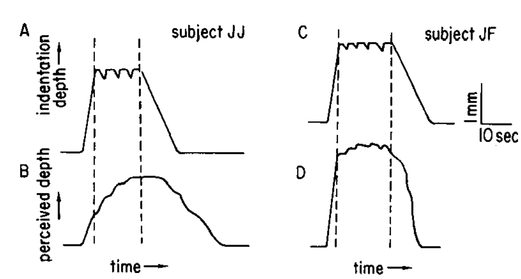

Figure 10. B and *D* show a "wind-up" type response in which there was an illusion that the indentation depth increased each time the partially retracted stimulator reindented to the same 2-mm depth. By the fourth indentation, the increase had reached 120% in *B* and 13% in *D*. Most of the wind-up errors had values intermediate between these two.

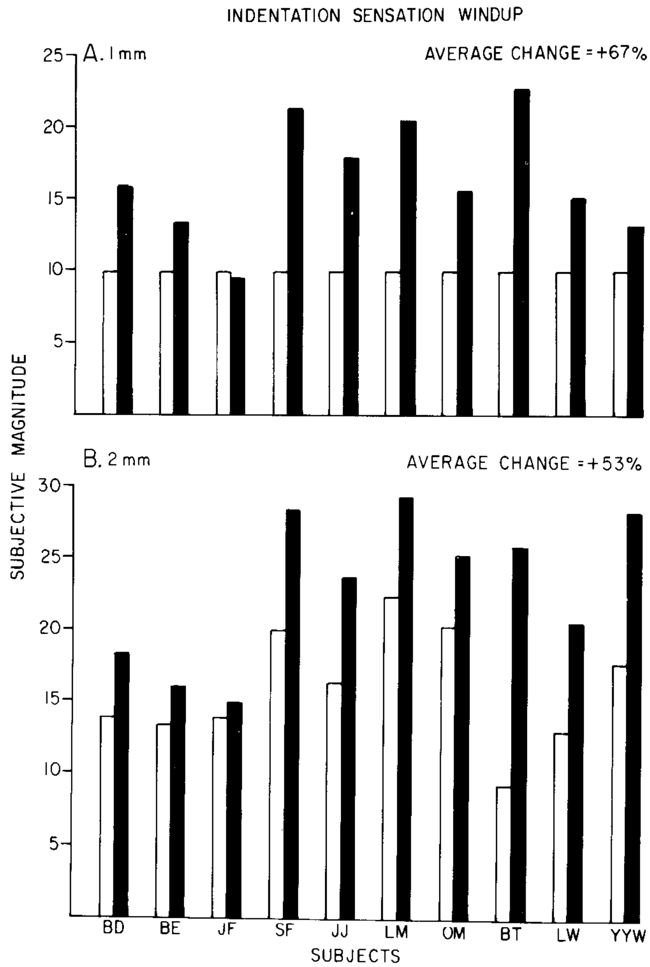

Figure 11. The *open bars* in *A* show the perceived indentation depth after the skin was indented 1 mm. The stimulator was then partially withdrawn (5 to 30%) and reindented to the same depth several times. The *solid bars* show the perceived depth during the fourth of these sequential indentations. The stimulator advanced at 0.4 mm/sec. Retraction rates varied from 0.33 to 0.08 mm/sec and were adjusted for each individual subject so that a good wind-up was obtained. The displacement in *B* was 2 mm. Stimulator advance was once again at 0.4 mm/sec and retraction rates varied from 0.29 to 0.11 mm/sec. The magnitudes in *A* and *B* were normalized as in Figure 9, and three to six repetitions of the stimulus were averaged to obtain each of the values shown in *A* and *B*. The average increases, 67% in *A* and 53% in *B*, were statistically significant ($p < 0.01$).

the fourth indentation in the sequence. Figure 11*B* is constructed similarly but, in this case, the indentations were 2 mm in amplitude. All 10 subjects showed wind-up at 2 mm (average increase 53%) and 9 of the 10 did at 1 mm (average increase 67%). Both increases were statistically significant ($p < 0.01$) and both were significantly larger than the increases during steady indentations of the same depth ($p < 0.01$, Fig. 9, *A* and *B*).[5]

[5] There were three subjects who sometimes did not increase their initial scaling when the stimulator depth was increased from 1 to 2 mm (BD and LW in Fig. 9 and BT in Fig. 11). The data for Figures 9*A* and 11*A* were collected in one session and the data for Figures 9*B* and 11*B* were collected in another. The instructions read to the subjects did not stress cross-session comparisons but, rather, accurate rendering of perceived depth during a particular stimulus (see "Materials and Methods").

Discussion

When mechanoreceptors are involved in signaling the position of a structure, the fact that they adapt would appear to degrade the signal. In the present experiments, we have studied subjects' perception of the degree to which their skin is indented (i.e., the position of the skin surface with respect to the deeper tissues) and have found that many actually make an overestimation error in which a stimulator that is steady is felt to be gradually indenting the skin. Although, on average, the errors were not large, this was an unexpected finding both because we expected more accurate depth judgments and because, on the basis of earlier work, the sensations produced by a skin indentation are generally thought to adapt (Zigler, 1932; Crook and Crook, 1935; Horch et al., 1975). Although the utility, if any, of overestimation errors remains obscure, there are two differences between these earlier studies and the present one which may account for the different findings. (*1*) The earlier work was done on hairy skin where depth sensations adapt more rapidly than they do on the fingertips (see Burgess et al., 1983), and (*2*) we have concentrated here on the initial part (first 12 to 20 sec) of a plateau indentation. A 1-mm indentation of the fingertip is still easily sensed after 2 min, although by that time subjects report that the stimulator indents the skin somewhat less than initially (an underestimation error, unpublished observations). An indentation of comparable depth on the forearm has completely faded from awareness by this time (Horch et al., 1975).

There is good evidence that human cutaneous mechanoreceptors adapt (Knibestöl, 1975). The fact that many of the subjects thought the indentation depth of the stimulator was gradually increasing while their cutaneous mechanoreceptors were adapting might be explained in a number of ways. Since it seems probable that skin indentation depth is signaled, at least in part, by the discharge frequency of receptors excited by the indenting stimulus (Burgess et al., 1983), a well known property of the nervous system, variously called recruitment (Morrison and Dempsey, 1942) or wind-up (Mendell and Wall, 1965), could sustain perceived indentation depth in the face of receptor adaptation. This is equivalent to postulating that an integration process (in the mathematical sense) goes on in the central neural circuitry responsible for judgments of skin indentation depth. A neural integration process in this sense is one where the excitation produced by an arriving impulse persists long enough so that it can add to the excitation produced by subsequent impulses, even though the integrator neuron(s) may have generated an action potential in the meantime. The changes produced by any given impulse are thought of as decaying at a certain rate (i.e. the integrator is "leaky"), so that little or no integration would occur if the impulses arrive at less than a certain frequency. Thus the subject-to-subject variability we observed in subjective estimation of skin indentation depth with time could be explained either by differences in receptor adaptation rate or by differences in the time constant of a central integrator.

If there is an integrator in the central circuitry for indentation depth judgments, and if the skin can move outward without discharging the integrator, then indentation depth judgments should "wind-up" during repeated reindentation to the same depth. Hayes noted in 1912 that "pressure" aftersensations are favored by slow removal of the stimulator. Consistent with her observation, we were able to demonstrate wind-up of perceived indentation depth most easily by reindenting the skin after a slow retraction. Wind-up is likely to reflect the action of a central integrator rather than increasing receptor discharge because previous studies have indicated that reduced responsiveness rather than wind-up is the rule when cutaneous mechanoreceptors are restimulated (Adrian and Zotterman, 1926; Bessou et al., 1971; Barker et al., 1982; Pubols, 1982). Moreover, an integrator could explain the observation (Burgess et al., 1983) that judgments of skin indentation depth are less rate sensitive than the responses of cutaneous mechanoreceptors.

Adrian (1928) postulated many years ago that activity in a single slowly adapting afferent fiber would produce a continuous sensation through the action of a neural integrator, and this insightful suggestion has direct bearing on a basic question in sensory neuroscience: the extent to which the central nervous system operates linearally on its inputs. Linear in this context means that $\Delta Y/\Delta X$ equals a constant, where ΔY is the change in the output of a central circuit in response to a change (ΔX) in the input to the circuit measured in impulses per second. If the central circuits are linear, the input-output characteristics of the system are set by the receptors. This would not be the case for skin indentation depth sensations if a central nervous system integrator converts the rate-dependent signals from the receptors into a largely rate-compensated awareness of altered skin position, slowing and smoothing the temporal profile of the input in the process so that receptor adaptation is compensated for. If neural integration is occurring, the relationship between the perceived depth of a stimulus and the frequency of mechanoreceptor discharge will depend on the duration of the stimulus; for example, a brief high frequency discharge may charge the integrator less than a lower frequency discharge of longer duration, and vice versa. As long as the input frequency exceeds the integrator decay rate, increasing the duration of the input will increase the perceived depth of the stimulus even though the input frequency is unchanged.

Our justification for spending some time exploring the properties of a neutral integrator for signaling skin indentation depth is that an integration process provides a simple and unifying explanation for the observations presently available on slowly adapting mechanoreceptors and skin indentation depth judgments. However, other explanations are possible, and just how skin indentation depth is signaled will not be properly known until the relevant central nervous mechanisms are scrutinized directly.

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